TRACHYPACHUS AND THE ORIGIN OF THE HYDRADEPHAGA (COLEOPTERA)[1]

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The specialized aquatic families of the Suborder Adephaga have often been united to form a Superfamily Hydradephaga, while the terrestrial families are included in a contrasting Superfamily Geadephaga. Basic to an understanding of the phylogeny of the Adephaga is a decision as to whether this separation is a natural one. In other words, have the Hydradephaga arisen from a primitive adephagan different from that which gave rise to the Geadephaga, or are the Hydradephaga simply Geadephaga modified for an aquatic existence?

Available evidence overwhelmingly supports the latter view. Crowson (1955) held that the basic features of the adephagan metasternum, hind coxae, and abdomen were originally adaptations for life beneath bark; while Bell and Bell (1962) suggested that they were, instead, adaptations for cursorial locomotion. In either case, there is nothing in the structure of Hydradephaga to preclude descent from early geadephagans. Moreover, the characters supposedly distinguishing the two groups are not entirely constant. All Hydradephaga lack pubescence on the outer antennal segments, but it is also lacking in the terrestrial Trachypachini (*Trachypachus* Motschulsky and *Systolosoma* Solier). Hydradephaga are often said to lack a transverse sulcus on the metasternum. In Hygrobiidae, however, there is a remnant of the sulcus, while in Haliplidae it is represented by a row of coarse punctures. On the other hand, the aberrant, bark-inhabiting Rhysodini (usually accorded family rank, but regarded as modified Carabidae by Bell and Bell, 1962) lack a transverse sulcus. The sulcus is the external opening to an internal ridge, evidently serving for muscle attachments; and its tendency to disappear in Hydradephaga and Rhysodini is probably a reflection of changes in methods of locomotion.

All Hydradephaga have hind coxal cavities of the interrupted type, in which the hind coxa extends laterally to the margin of the body, eliminating contact between the metathoracic pleurites and the first abdominal sternite. Coxal cavities of this type occur also in Trachypachini and in *Gehringia* among terrestrial Adephaga. In the latter genus, this feature seems to be connected with the lateral displacement of the hind legs, while in Trachypachini and the Hydradephaga it is necessitated by the great enlargement of the coxae themselves.

Hydradephaga universally lack an antenna-cleaning organ on the anterior tibia. A secondary loss of this structure would be expected, how-

ever, in the aquatic environment, where antennae are unlikely to become soiled. It has also been lost in the terrestrial Paussini, which have highly modified antennae unsuited to an antenna cleaner. Specialized tactile setae are apparently universal among Geadephaga, while they are sometimes said to be absent in Hydradephaga. Loss of tactile setae is a change that one would expect in a geadephagous beetle adapted for life in water, since such setae would increase friction during swimming. In *Haliplus triopsis* Say, however, there is a pair of well-developed tactile setae on the mentum, much like those of most Carabidae. Remnants of the system of tactile setae should be searched for in the other families of Hydradephaga.

If it is concluded that Hydradephaga have arisen from the Geadephaga, the next question is whether they represent a single invasion of the aquatic habitat, or multiple invasions. In other words, are the Hydradephaga a monophyletic group? Strong contrasts in the adaptations for aquatic life in both larvae and adults suggest that three separate invasions occurred. (Crowson, 1955, and Leech and Chandler, 1956, discuss these adaptations.) Dytiscidae, Hygrobiidae, Amphizoidae, and Noteridae (often included in Dytiscidae) seem to form a monophyletic group. In these families the larva has lost the apical portion of the abdomen, the ninth segment being vestigial or absent. In most species, the larva breathes air at the surface through the enlarged spiracles of the eighth abdominal segment. (In Noteridae, the abdomen is secondarily adapted for piercing air spaces in the stems of aquatic plants; in Hygrobiidae and in the dytiscid *Coptotomus* Say, there are tracheal gills on the abdomen; in Hydroporinae neither gills nor functional spiracles are present, and respiration is apparently cutaneous. All of these exceptional groups have an abbreviated abdomen, suggesting derivation from a species which breathed at the surface.)

In Gyrinidae, in striking contrast, the larval abdomen is much like that of Carabidae, the tenth segment forming a well-developed pygopod armed with hooks. The urogomphi are well developed. Each abdominal segment (except the tenth and, sometimes, the ninth) has a pair of lateral tracheal gills. The spiracles of the eighth segment are not enlarged, and the spiracles are not used at all except, perhaps, when the larva emerges on land to pupate. The larvae have a strong similiarity to those of Corydalidae (Order Megaloptera). For this reason, Bradley (1930) suggested that the Gyrinidae should be regarded as the most primitive living beetles. It seems more likely, in view of the highly specialized nature of adult Gyrinidae, that the larvae show a strong degree of evolutionary convergence with those of Corydalidae. Gyrinid larvae, in any case, show no convincing evidence of relationship to the preceding families (which will be referred to for brevity as the "dytiscoid" families).

In the Haliplidae, the spiracles are not used in larval respiration, oxygen being obtained directly through the skin, in some cases supplemented by scattered, rodlike outgrowths of the body wall. Although the tip of the abdomen is somewhat reduced (the urogomphi are absent, and the tenth segment, if present, is only a vestige, not forming a pygopod), it is less so than in the dytiscoid families. The spiracles of the eighth

segment are not enlarged. The spiracles, according to Crowson, are not used except possibly in the last instar of some species. The haliplid larva, like the gyrinid one, appears far more likely to have evolved directly from a terrestrial form than from a larva of the dytiscoid type.

The aquatic adaptations of the adult Hydradephaga support the thesis of three separate invasions. The Haliplidae are unique in having large platelike extensions of the hind coxae, which more or less conceal the abdominal sternites, and which form an air storage chamber. On the other hand, the legs of Haliplidae are scarcely modified for swimming, except for the presence of a row of swimming hairs on the tibia.

In the dytiscoid families, with the exception of Amphizoidae, the front and middle legs play no part in swimming, being adapted for clinging to objects, grasping prey, and climbing emergent vegetation preparatory to flight. The hind legs are highly adapted as paddles, being elongate, more-or-less compressed, and fringed with stiff swimming hairs. In Amphizoidae, the legs are closer to a typical geadephagous type. The hind tarsi are scarcely compressed, and their claws are large and divergent. All three pairs of legs are used in walking on the bottom of cold, swift mountain streams. According to Edwards (1951), the hind legs show vestiges of swimming hairs, suggesting derivation from a swimming dytiscoid ancestor. Since amphizoids live in a habitat where swimming is hazardous, a secondary loss of swimming adaptations would not be surprising.

The Gyrinidae are unique in that both middle and hind legs are adapted for swimming, while the front legs are highly specialized grasping organs. Moreover, the legs are adapted as paddles in a manner completely different from that of the dytiscoids. Each tibia has a broad, thin expansion on its outer margin. The distal margin of the expansion contains a deep slot into which the upper margin of the tarsus is fitted. The tarsus, which is extremely short and compressed, can be disengaged from the slot, a feature which might facilitate its use in terrestrial locomotion.

The anatomy of both adults and larvae, then, favors the theory of three separate invasions of the aquatic habitat. To what group of terrestrial Adephaga is each of these phyletic lines most closely related? Among the Carabidae, the Trachypachini show the most points in common with the Hydradephaga. It is worth considering, therefore, whether this tribe is really related to any or all of the Hydradephaga. There have been two sharply contrasting theories about the relationships of Trachypachini in recent years. Jeannel (1941) placed Trachypachini with Metriini, Ozaenini, Paussini, and Gehringiini in a major subdivision of the Carabidae, the Series Isochaeta. (Jeannel ranked the above tribes as families, and elevated the Carabidae to the rank of superfamily. Since most other workers have not accepted the change in ranks, it will minimize confusion if his rank changes are not adopted in this discussion.) Crowson (1955), on the other hand, has given the Trachypachini family status and has regarded it as intermediate between the Geadephaga and Hydradephaga.

Jeannel's theory is supported by the structure of the antenna cleaner of *Trachypachus*. It is of the typical isochaetous type, in the form of an

emargination of the inner face of the anterior tibia, with both tibial spurs distal to it. (In the vast majority of Carabidae the antenna cleaner lies between the tibial spurs, and the posterior spur is more or less displaced proximally.) It agrees closely with the antenna cleaner of Metriini and Ozaenini. (Paussini, despite the absence of a well-developed antenna cleaner, are placed in the Isochaeta because there is other evidence for a relationship with Ozaenini—see Darlington (1950); Gehringiini do not have a typical isochaetous antenna cleaner and are probably not Isochaeta at all—see Bell (1964).) A further point of similarity between Trachypachini and the other Isochaeta is the presence of about twelve, rather than six, tactile setae on the labrum (Bell, 1964). To my knowledge, a doubling of the labral setae has not occurred in any other group of Adephaga in which the mouthparts are unspecialized. It does occur among Cicindelini, or at least some of them. In the latter group, however, the mouthparts, including the labrum, are strikingly different from those of other Adephaga. At any rate, the doubling of the labral setae is not obviously functionally related to the structure of the antenna cleaner, and the two characters together make a strong case for placing *Trachypachus* among the Isochaeta.

Two functionally unrelated characters, the absence of antennal pubescence and the presence of hind coxal cavities of the interrupted type, make a case for relating *Trachypachus* to the Hydradephaga. The first
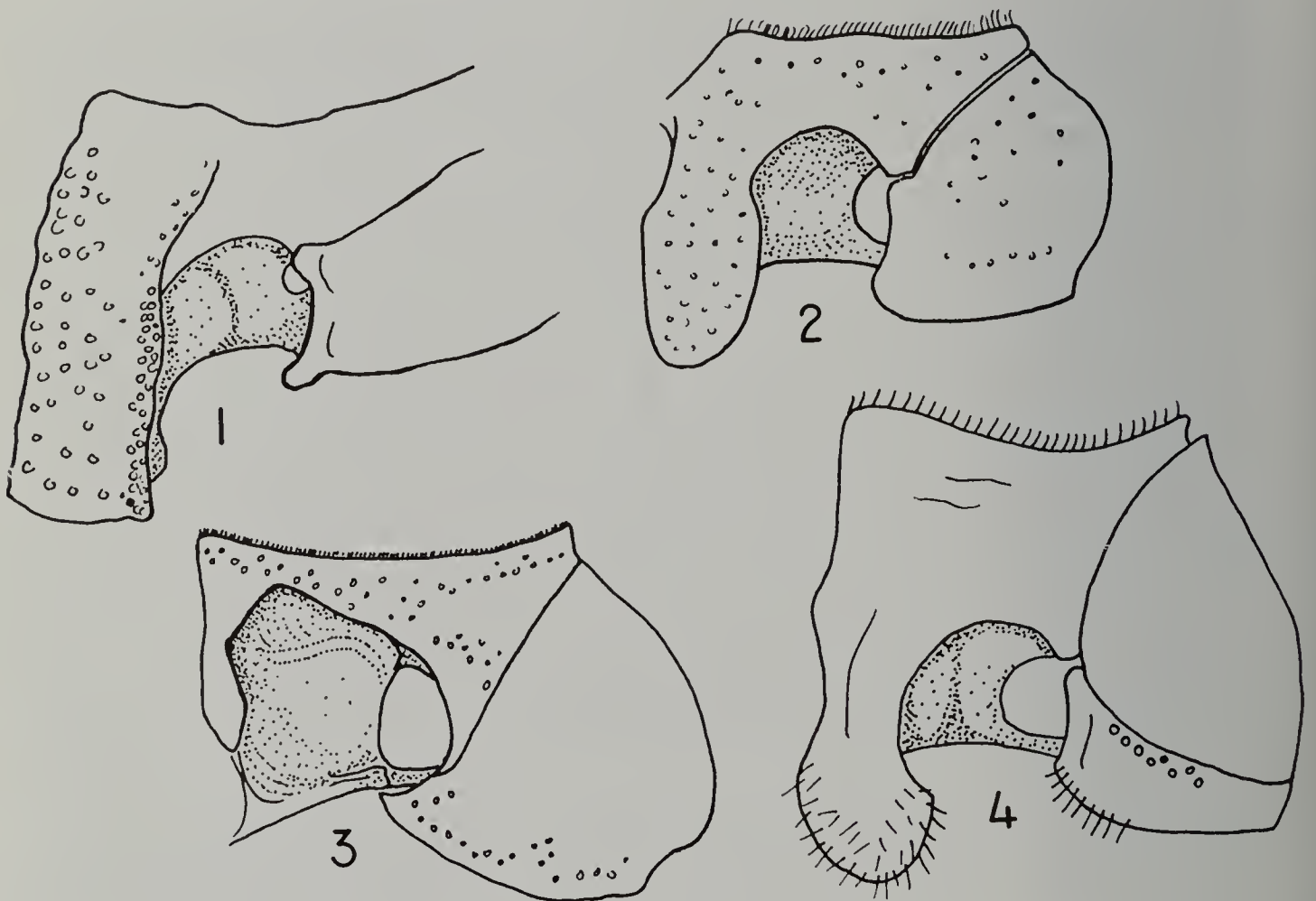
Figures 1-4. Left anterior coxal cavity, viewed obliquely. 1—*Haliplus triopsis* Say (Haliplidae). 2—*Amphizoa insolens* Lec. (Amphizoidae). 3—*Dineutes discolor* Aubé (Gyrinidae). 4—*Trachypachus gibbsi* Lec. (Carabidae).

character is restricted to the groups mentioned; the second is shared only with the Gehringiini. I have discovered a third character to be added to the list: in *Trachypachus,* as in all Hydradephaga so far dissected (*Haliplus, Amphizoa, Agabus, Laccophilus,* and *Dineutes*), there is a similar type of anterior coxal cavity (figs. 1-4). All have a *postcoxal bridge,* a thin bridge of sclerotized exoskeleton immediately posterior to the opening between the prothorax and coxa. This structure should not be confused with a *postcoxal bar,* which is found in those Adephaga with closed coxal cavities. A bridge is part of the primary body wall and therefore consists of a single thickness of exoskeleton. It is entirely hidden unless the coxa is removed from the cavity. A bar consists of two tubular outgrowths of the body wall united at their tips, one from the proepimeron and the other from the prosternum. It is heavily sclerotized and is visible externally. (I shall publish an extensive paper on the coxal cavities of Adephaga in the near future; a preliminary report (Bell, 1965) on this work has already been published.) Many Carabidae have both a bridge and a bar (Carabidae Biperforatae as defined by Sloane, 1923); but *Trachypachus* is the only carabid in which the bridge occurs without the bar, i.e., with open coxal cavaties. Thus there are three apparently unrelated characters shared by *Trachypachus* and the Hydradephaga, indicating the likelihood of a common ancestry.

Lindroth (1960) discovered the larva of *Trachypachus gibbsi* Lec. It is a typical terrestrial adephagous larva, living in dry sand and without any aquatic adaptations. The only feature it seems to share with the larvae of Hydradephaga is the absence of a ligula on the labium. A ligula is also absent in various terrestrial larvae, including *Brachinus, Lebia, Gehringia,* and Rhysodini. Lindroth considered that the terrestrial nature of the larva precluded any relationship with the Hydradephaga, and that the absence of the ligula, together with the incomplete hind coxal cavities of the adult, was evidence of relationship to *Gehringia.* For reasons stated above, I doubt the relationship of *Gehringia* to the Isochaeta, and that the absence of a ligula is significant evidence for it, since the ligula has been lost in many groups of Adephaga. The terrestrial character of the larva does not preclude relationship to the Hydradephaga, but it does suggest that *Trachypachus* is not descended from fully aquatic ancestors. This is consistent with the evidence previously presented, that the Hydradephaga made three separate invasions of the water.

The most reasonable explanation of the origin and relationships of the Hydradephaga is as follows:

1. The Hydradephaga do not constitute an independent phyletic line of Adephaga, but are Isochaeta modified for an aquatic existence. As in the case of the Paussini, this is not indicated by the possession of obvious isochaetous characters, but rather by clear indications of relationship to an undoubted member of the Isochaeta.

2. The Hydradephaga represent three phyletic lines: the Haliplidae, Gyrinidae, and the complex of dytiscoid families. Each of these lines became adapted for aquatic life independently. Each of these lines is as closely related to Trachypachini as it is to the other lines. Hydradephaga is therefore not a natural group unless it is defined so as to in-

clude Trachypachini. In this case, the name is inappropriate and misleading. I suggest the substitution of "Glabricornia," based on the lack of antennal pubescence, the most obvious common character of the group.

3. The common ancestor of the Glabricornia was a terrestrial, isochaetous adephagan, with open, bridged anterior coxal cavities and incomplete posterior ones, and with glabrous antennal segments. In all important characters it resembled the modern *Trachypachus*. The larva was a typical terrestrial adephagous larva (except, perhaps, in having lost the ligula). Although both adult and larva were certainly not aquatic, they may have been more hygrophilous than the living species of *Trachypachus*.

4. *Trachypachus* is an extraordinary phylogenetic relict, having survived almost unchanged from the time of origin of the Glabricornia. The Chilean *Systolosoma* should be investigated to see if it is really closely related to *Trachypachus*, or if it represents an independent line of persistently terrestrial Glabricornia.

It would require a wholesale rearrangement of the formal classification of the Adephaga to make it express accurately the interrelationships of the Isochaeta and the Glabricornia. Eventually it will be desirable to do so. At present, the interrelationships of terrestrial Adephaga are poorly understood and frequently debated. I decline, therefore, to propose any changes in family boundaries at the present time.

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